

SIGNIFICANCE OF FOSSIL POLLEN FOR ANGIOSPERM HISTORY¹

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ABSTRACT

The significance of fossil pollen evidence for 139 families for understanding the evolutionary history of the angiosperms is discussed. Deficiencies in the fossil record and uncertainties in its interpretation are stressed. The transition from gymnospermous ancestors is as yet unknown. The earliest lower Cretaceous angiosperm pollen types, although few in number, indicate considerable taxonomic diversity. The succeeding progressive differentiation is clearly shown by the pollen as well as by the macrofossil record. The competitive replacement of ancient gymnosperms and ferns by angiosperms was largely completed in the Turonian. Strong differentiation takes place in the Maestrichtian and most higher taxonomic categories were present by the end of the Cretaceous. Differentiation at lower taxonomic levels continued in the Tertiary. Some taxa are discussed more in detail and are shown to have different timing and patterns of development. Dicotyledonous herbaceous types appear relatively late and, in the monocotyledons, the woody palms are a secondary development. In general, a positive correlation exists between advancement index and time of first appearance. Some evidence for evolution by gradual development, as well as by punctuated equilibria, is discussed.

The significance of fossil pollen for the study of an angiosperm evolution is based primarily upon its abundance and its characteristic and diversified morphology. The first provides us with a nearly continuous, often independently dated stratigraphical record and the second with a biased and incomplete taxonomical record.

Let us look at this bias first. It is evident that some pollen types have a better chance of being preserved in the fossil record than others, and this depends mainly on quantity produced and distance between source area and place of sedimentation. Thus, a wind pollinated dominant in the coastal vegetation is more likely to leave a fossil pollen record than a rare, montane, insect pollinated plant. Based on this, it has been argued by Axelrod (1970) and Stebbins (1974) that the pollen record essentially shows only the penetration of angiosperms into the lowland and coastal environment but that they must have originated elsewhere and that the main features of fossil pollen evolution only reflect adaptation to advanced pollination syndromes.

To a certain extent this is true and tends to indicate a first date that is too young, unless the fossil evidence indicates that the transition from an ancestral type has taken place in or close to the area of sedimentation, as in Juglandaceae or Sonneratiaceae. Pollen evolution itself is only partly related to pollination, however. Recent

studies by Heslop-Harrison (1976), Muller (1979), Payne (1981), Bolick (1981), and Hesse (1981) have indicated a large diversity of functions for the exine, such as adaptations to hermogamy, storage of recognition substances and of lipids, which have been linked, next to pollination, to the extreme diversity of present-day exine structure in angiosperms. It was already apparent from the first investigations of the fossil pollen record that the evolution from simple to complex types in response to these factors can be traced in surprising detail. In fact, a close analysis of the morphology of fossil types in comparison with form and function in recent equivalents will allow us to detect the evolution of many adaptations in the reproductive sphere.

To demonstrate how far function may determine the morphology of the exine, two series of photomicrographs of Recent pollen types, with contrasting morphology are presented. First, alder pollen (Fig. 1a, b) is relatively small, dry, thin walled, with 4 or 5 small pores and an intragranular exine structure. Here the main hermogathic movements are being absorbed by the ridge-enclosed flexible wall, which is quite typical of anemophilous pollen in general. Next, *Cobaea* (Fig. 1c-f) has a large, periporate pollen grain obviously adapted to insect pollination. It has a thick, rigid wall, in which stress is absorbed all over equally, resulting in a spherical shape.

¹ The author is much indebted to M. Zandee (Department for Theoretical Biology, University of Leiden) for the statistical evaluation of the relation between age and advancement index. Requests for reprints should be addressed to the Director, Rijksherbarium, Schelpenkade 6, 2313 ZT Leiden, The Netherlands.

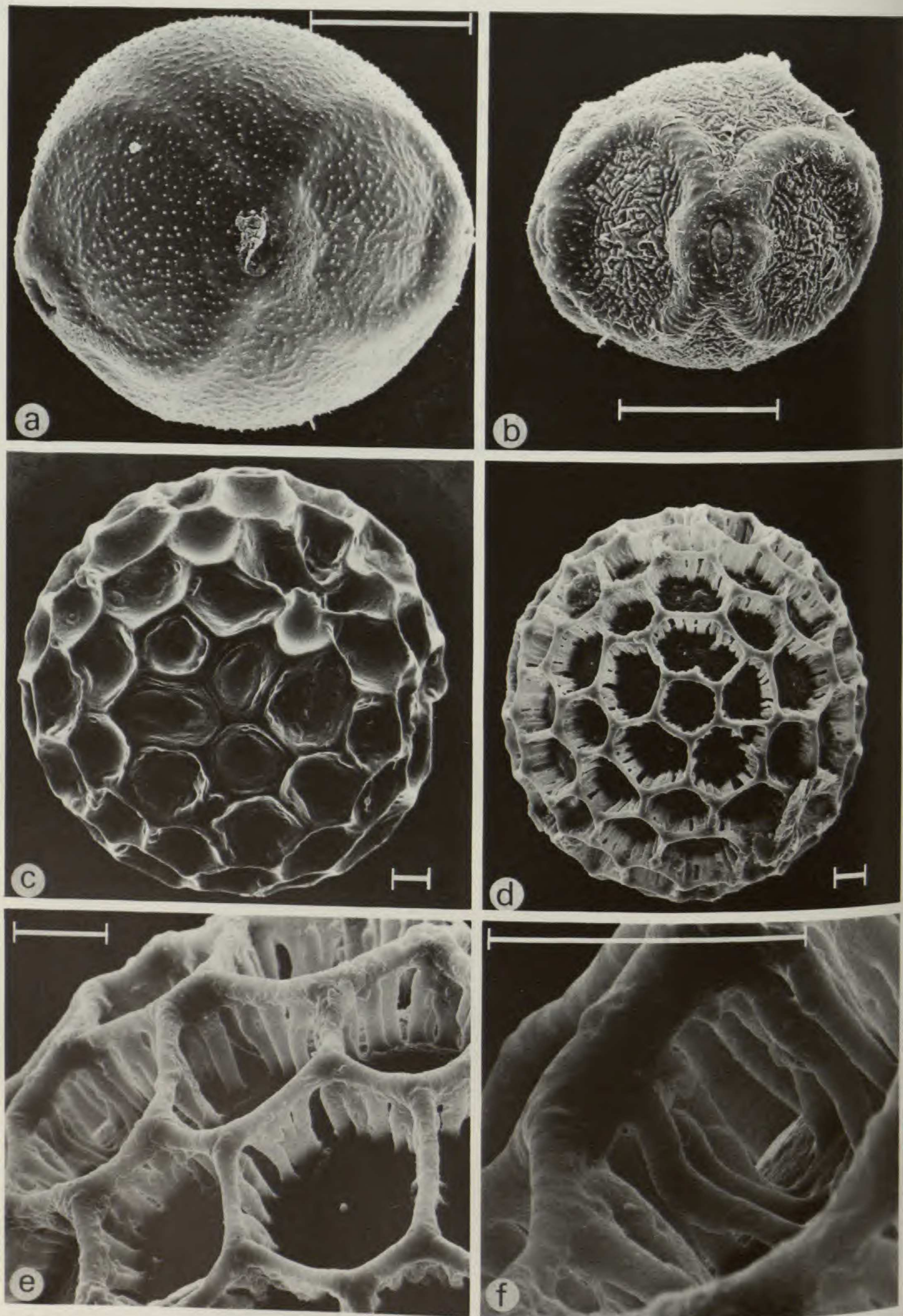


FIGURE 1. a-b. *Alnus glutinosa* pollen (Betulaceae), fresh, exine surface dry.—a. Expanded, upon release from anther, $\times 2,500$.—b. Contracted after two days exposure to sunny atmosphere, causing the arcuate thickenings to stand out as a rigid framework supporting the withdrawn, thin, and flexible exine. The apertures are

The beautiful open structure of the exine is, in the living state, covered with oil, making the grain both sticky and insulated against water loss. It may have evolved both in response to stress accommodation and oil retention. These examples show that many structures of fossil pollen grains can be interpreted better if comparable Recent pollen types are studied more in detail with regard to their functioning.

However, there is also a non-functional (non-mothetical) element in pollen morphology that arises as a consequence of limitations and repetitions in design due to certain mathematical plus physical restraining factors during development (Muller, 1980; Melville, 1981). Such characters are, in their evolution, more independent of biological functioning, and thus are probably more useful for recognition of taxa and their phylogenetic relationships, as first shown by Van Campo (1967) in her study of the successiform series.

Although taxonomic identification will rely on as many independent characters as possible, it is clear that morphologically specialized pollen types stand a better chance of being recognized and that families of angiosperms that have retained an unspecialized pollen type are consequently underrepresented in the fossil record. This is especially serious if pollen specialization lagged behind the evolution of other characters due to mosaic evolution (heterobathmy). It will be clear that the factors influencing pollen evolution are quite distinct from those acting on anatomical, leaf, fruit, or seed characters. This, however, can rarely be proven in the fossil record, although most of the cases in which a discrepancy in time of first occurrence has been found between macro- and microrecords are probably due to this phenomenon. It may be significant that in the few fossil flowers found with pollen, some showed a combination of characters not known in the Recent relatives.

The most clear-cut case is perhaps *Burretia* from the Miocene of Europe, described by Mai (1961). The flower characters indicate affinity with the subfamily Brownlowioideae of Tiliaceae, whereas the pollen is of the *Tilia* type, restricted at present to the subfamily Tilioideae. In *Fa-*

gopsis from the lower Oligocene of the United States (Wolfe, 1973), *Quercus* type pollen is found in betulaceous staminate inflorescences, associated with fagaceous leaves. Tiffney (1977) has found a flower in the upper Cretaceous that contains tricolpate pollen but has a combination of characters that cannot be matched in the living angiosperm flora. From the mid-Cretaceous, Dilcher (1979) has reported monocolpate-reticulate pollen from catkins of an amentiferous type, a most unusual association, almost suggesting that the older the fossil, the more unusual the combination. Some of these fossils undoubtedly belong to extinct taxa, which may or may not have given rise to lineages leading to Recent ones.

In general, it may be stated that the degree of precision in identification decreases in proportion to the age of the fossils. This is not to be confused with the chance for an erroneous identification, but rather that the circle of possible affinity increases. Thus, although in the Tertiary generic identification is often possible, in the Cretaceous we may only be sure of affinity at the family or even higher taxonomic level.

In the following discussion all these potential sources of error have been taken into account as far as possible. It proceeds, in general, on the assumption that with a large, statistically significant number of identifications per taxon, at least some estimate of time of origin and development is possible. Whereas in 1970 (Muller) only 74 families with 135 pollen types could be identified based on fossil pollen, in 1981 (Muller) 139 families with a total number of 332 pollen types could be identified. The present account will deal principally with the general results of this last compilation, with the addition of some important new records published recently.

It is self-evident that these pollen records should be combined with macrofossil evidence for a final interpretation, and it is hoped that critical lists for leaf, seed, fruit, and wood remains will become available in the near future.

Some remarks on nomenclature and classification of fossil angiosperm pollen should be added because this will have to reflect the degree of precision of the identification. Apart from those rare cases in which a fossil pollen grain can be

well protected against collapse by the annular thickenings, $\times 2,500$. c-f. *Cobaea scandens* pollen (Polemoniaceae).—c. Fresh, covered with a sticky, oily deposit ("pollenkitt"), $\times 500$.—d-f. Acetolyzed, showing the open, columellate structure, supporting the inner wall in which regularly distributed circular pores are located at the bottom of the smaller lumina. d, $\times 500$; e, $\times 1,500$; f, $\times 4,000$. Line equals $10\ \mu\text{m}$.

identified with a living species, it should be placed as a form species in either a Recent genus, a form genus, a Recent family, or a higher taxonomic category. In the case of extinct groups of pollen, the higher taxonomic category must be circumscribed exclusively on the fossil evidence but should be related to the general classification even if only by stating that they are angiospermous. Thus, the group of Normapolles should have at least ordinal rank and can be placed in Hamamelidanae; the genus *Aquilapollenites* plus associated genera could form an extinct monotypic family within Santalales. *Tricolpites micromunus* from the lower Cretaceous can be identified with Magnoliopsida B-G, for which, unfortunately, no taxonomic name exists, and *Wodehouseia* is an extinct incertae sedis genus in the Angiospermae. At the other end of the scale *Florschuetzia trilobata* could represent an extinct genus linking Lythraceae and Sonneratiaceae.

This approach is based on the very sensible recommendations made by Schopf (1969) and allows us to integrate both fossil and Recent angiosperms in one system of knowledge. This approach certainly allows incorporation of corrections when new evidence comes to light and avoids the reproach made against many leaf identifications with Recent genera with its attendant dangers [see Wolfe (1973) and Hughes (1976) for a pertinent critique of this habit].

Of course, neutral names are preferred for fossil pollen types, and names like *Nothofagidites*, or *Santalumidites* should be avoided at all cost, since they, more than anything else, suggest too strongly what can only be tentative suggestions of affinity.

ORIGIN AND EARLY DEVELOPMENT (BARREMIAN-ALBIAN)

Because at this symposium the pollen floras from this period are dealt with in detail by other contributors, and because my approach of tracing Recent pollen types backward in time virtually denies me the possibility, as has been rightly emphasized by Stebbins (1950) and Hughes (1976), of recognizing the vital link between gymnosperms and angiosperms, I must restrict myself to a few remarks only about the earliest phase of angiosperm evolution.

In 1975, Doyle et al. presented their well known scheme that could form a basis for separating fossil gymnospermous from angiospermous exines. However, the discovery by Cornet (1980,

1981), of pollen grains with columellate structure from the Triassic, which are unfortunately not yet described in detail, casts doubt on the validity of at least one criterion leaving only that of the laminated endexine, which is very hard to test in fossil material.

At least three different functions have been proposed for the columellate exine, so beautifully developed in *Cobaia* pollen (Fig. 1c-f). These are: to hold pollenkit and lipid material in connection with entomophily and for sealing purposes; to store recognition substances for stigmatic germination; and to give structural support in connection with harmomegathy. It will therefore be difficult to determine the ecologic significance of the columellate structure for Cornet's Triassic grains. All known living entomophilous gymnosperms have sticky pollen grains but lack columellate or even alveolate exines, according to Frederiksen (1980). However, Hesse (1980) has recently commented on the lack of pollenkit in many gymnosperms. In angiosperms pollenkit deposited on the tectum surface renders the pollen sticky, but if it is deposited in the tectum cavities the pollen becomes powdery (Hesse, 1980). This is contrary to prevailing opinion that the reticulate-columellate exines invariably indicate stickiness and hence entomophily. In this connection it is of interest that Klaus (1979) has found evidence for relicts of columellate structure in *Pinus*. The columellate structure of *Clasopollis* is also well known, suggesting that the difference may not be fundamental.

If the Triassic columellate grains have been produced by ancestral angiosperms, then this structure may have been lost, probably because the group became extinct, to reappear with the first undoubted angiosperms in the lowermost Cretaceous. If not, we may have a case of structural parallelism between gymnosperms and angiosperms, likely to be due to structural or stickiness adaptations.

The first recognizable angiosperm pollen type is *Clavatipollenites*, starting in the Barremian. Thanks to detailed studies by Doyle et al. (1977), Hughes et al. (1979), and Walker and Walker (1980), it is clear that different types are involved. At least one form, *C. hughesii* appears to be closely similar to Recent *Ascarina* pollen and can in fact be traced to the Recent area of distribution (Muller, 1981, fig. 1). This pattern indicates a gradual range restriction with an essentially unchanged pollen morphology and hence probably also a similar pollination biology. In

Recent Chloranthaceae, e.g., in *Hedyosmum*, large amounts of pollen are produced and it seems likely that the *Clavatipollenites-Ascarina* lineage may have been adapted to an unspecialized pollination both by wind and indiscriminate insect visitors. According to Dilcher (1979) this may represent a basic and primitive strategy in angiosperms. True anemophily with dry, powdery pollen would be a secondary specialization from this initially indiscriminate system and may, according to Dilcher (1979), already have existed in mid-Cretaceous time.

Of course no evidence exists regarding the other characters of the plants producing these early *Ascarina*-like pollen types; but that they belonged to the ancestral complex of Chloranthaceae, or if one would add some more caution, of Laurales appears highly probable.

Other grains belonging to the *Clavatipollenites* complex may be ancestral to Myristicaceae, according to Walker and Walker (1980), but these have not yet been traced to younger occurrences.

Recently, however, a significant discovery has been made by Walker et al. (1983), who described undoubted Winteraceae pollen tetrads from the late Aptian/early Albian of Israel. This takes the record for this family back another 35 Ma compared to the late Cretaceous record listed in Muller (1981), indicating that taxonomically not closely related members of the Magnoliidae were already present in the lower Cretaceous, thereby suggesting a much earlier, possibly Jurassic origin and differentiation of this primitive subclass of Angiospermae.

The second main angiospermous pollen type to appear is the tricolpate reticulate type in the Aptian. Like *Clavatipollenites*, it is small and similar in the columellate exine structure but has three equatorial colpi. It is more likely that this change in apertures is related to improved harmomegathic efficiency and pollen/stigma interaction rather than to a change in pollination. The small size of the pollen would indicate small flowers (Muller, 1979; Dilcher, 1979: 323), or anemophily (Crepet, 1981).

In contrast to the *Ascarina* type, this group of tricolpate grains can be identified only as having been derived from non-magnoliid dicotyledons. Today, it occurs in Ranunculidae (Menispermaceae predominantly, but also in Berberidaceae, Papaveraceae, and Fumariaceae), lower Hamamelididae (Trochodendraceae, Tetracentraceae, Hamamelidaceae, and Platanaceae), and Dilleniidae (some Dilleniaceae, some Salicaceae,

Brassicaceae). It appears to be rarer in Rosidae (some Oxalidaceae and Olacaceae) and very exceptionally is found in Asteridae (some Verbenaceae and Lamiaceae).

Thus the probability that the earliest Cretaceous tricolpate grains represent ancestral Ranunculidae and Hamamelidae appears higher than that they indicate the presence of early Dilleniidae or Rosidae.

The retention of this basic pollen type in so many Recent genera of diverse affinity is another striking example of "stasis" in pollen evolution and presumably also in pollination biology.

Rather soon after the first appearance of the tricolpate type, endoapertures developed in the Albian. The resulting tricolporate-reticulate pollen types represent a significant advance and specialization both in harmomegathic structure and increased efficiency of pollen/stigma interaction because of the presumed development of specialized intine structures. As stressed by Wolfe et al. (1975), this change has probably occurred independently in several lineages of the ancestral tricolpate complex. Menispermaceae, Flacourtiaceae, and Dilleniaceae have retained the transitional stages, the former having advanced less than the latter two families. In Rosidae, however, tricolporate-reticulate types have become dominant today. Thus, identification of these early tricolporate types is possible only in a very general way and probably indicates the presence of ancestral Dilleniidae and especially Rosidae.

The third main early angiosperm pollen type is the monocotyledonous one, recognized already by Doyle in 1973 from the Aptian. Functionally it is similar to the *Clavatipollenites* group of types.

Several other monocolpate types with a peculiar exine structure, such as *Stellatopollis* with a crotonoid pattern, or types found by Hughes et al. (1979) with a dipterocarpoid pattern, might also be monocotyledonous but disappear from the record soon afterwards.

A fourth main category is the periporate group from the Albian, identification of which is also very uncertain at present. This group is probably not related to Caryophyllidae and shows more similarity to *Alisma* (Alismataceae) and *Triemenia* (Monimiaceae), but has not yet been connected with younger types.

Thus, in the Barremian-Albian early phase of angiosperm development a limited number of taxa, but with a rather wide variety in pollen structure, make their appearance, roughly cor-

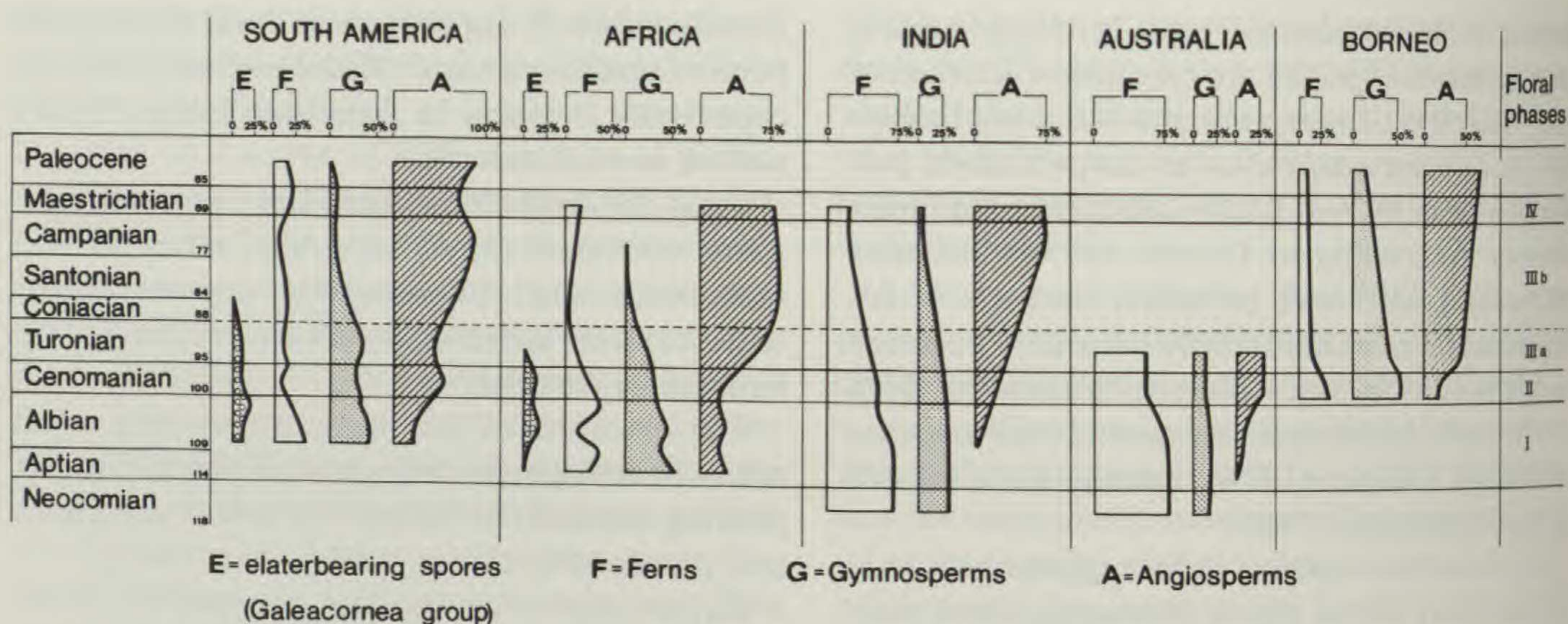


FIGURE 2. Microfloral diversity curves expressed as % species composition for four major categories of spores and pollen. Floral phases based on Muller (1981).

responding with increases in leaf diversity and abundance as Doyle (1977) and Doyle and Hickey (1976) have pointed out. This would appear to invalidate Axelrod's (1970) claim that fossil pollen does not register early angiosperm diversity. But, if, as Stebbins (1974) contends, angiosperm origin took place in a semi-arid dry land environment, admittedly palynology would only rarely detect traces of it, although the abundance of very early angiospermous pollen types in the ancient, probably semi-arid rift valley sediments of Gabon could support Stebbins' views, as already pointed out by Doyle (1977, 1978).

INCREASE IN ABUNDANCE (CENOMANIAN-TURONIAN)

The long known and well established increase in abundance of angiosperm macrofossils in the Cenomanian is accompanied by a comparable increase in pollen abundance and diversity. As shown in Figure 2, pollen diversity curves from many areas, in which no angiosperm macrofossils have been found at all, show a general picture of the intense competition between the young and vigorous angiosperms and the long established gymnosperms and ferns. These curves confirm Raven and Axelrod's (1974) and Doyle's (1978: 23) views of an early development of angiosperms in West Gondwanaland and negate Smith's (1970) and Takhtajan's (1969) view that the area between Assam and Fiji was the cradle of the angiosperms. Both Borneo and Australia appear to have been backwaters, far removed from the mainstream of early angiosperm development and, moreover, as now has been dem-

onstrated by plate tectonics, widely separated at that time. In Australia especially, the delayed entrance of angiosperms, possibly due to a cooler climate, is clear (Dettmann, 1981).

In the Cenomanian, the main new development in pollen evolution is the appearance of triporate types. This has probably taken place independently, in a lineage from tricolporate types via a flattening of the triangular shape and a shortening of the colpi to early Normapolles as first described by Doyle (1969) from the Cenomanian of the gulf coast of the United States and in the Turonian in a separate lineage leading to early triporate celtoid pollen types of which the derivation and place of origin are not yet known (Muller, 1968). The Normapolles group will be shown to have probably given rise to juglandaceous types, and the celtoid types have become fairly early established as Urticales. In both cases, ancestral types to higher Hamamelidae must have been present.

It is mainly in the Turonian that the real increase in pollen morphological diversity becomes obvious and that modern types quite suddenly appear, like that of *Ilex* (Celastranae) and *Gunnera* (Myrtanae). Such sudden appearances without any preceding ancestral types strongly suggest immigration into an environment in which they are more likely to be preserved than the place of their actual origin.

By the end of the Turonian the ecological breakthrough of the angiosperms appears largely to have been completed, but the taxa present were, in most cases, different from Recent ones, as is becoming also more and more clear from the study of macrofossil records. Tiffney (1981)

has suggested that this increase is a result of competitive pressure by increasingly efficient angiosperms, after a slow and gradual additive process of evolution during the lower Cretaceous, and has pointed out that many of the more archaic gymnosperms became extinct worldwide at the same time. The fossil pollen evidence is well in accordance with this view.

MAESTRICHTIAN EVENTS

In the Maestrichtian, an accelerated development of modern pollen types appears to have taken place indicating increased differentiation at the level of families, orders, and superorders (Muller, 1981, fig. 3). In view of the relative short duration of this period and also because this development clearly antedates the catastrophic events at the Cretaceous-Tertiary boundary, a special explanation appears necessary. Whether the phenomenon is due to a solar radiation maximum as postulated by Hughes (1976) or to co-evolution with insects and dispersal agents, the development of chemical defenses, or any other factor, is difficult to decide without further detailed study, although selective pressure on pollen evolution undoubtedly has become high.

The Maestrichtian is also the last period in which, locally, extinct groups of plants, such as those that produced the Normapolles types or *Aquilapollenites* were dominant. In the Australian-Antarctic region, in contrast, no comparable extinction has occurred and the flora developed early into a vegetation type that largely still survives today (Proteaceae, *Nothofagus*).

It is clear that differentiation at ordinal and superordinal level decreases in the succeeding Tertiary, but that at the family level much differentiation still took place, as was also emphasized by Tiffney (1981) for the Paleocene/Eocene and Eocene/Oligocene transitions.

For the ordinal level, this is shown in Figure 3 as a cumulative curve in which we can distinguish an initial slow rate, then a fast, tachytelic phase in the upper Senonian, followed by a slow but steady increase in the Tertiary.

DISCUSSION OF SELECTED TAXA

We can apply this method of analysis to the fossil pollen data, as well as to more restricted taxonomic groups among the angiosperms. This is especially illuminating if abundant and well-preserved pollen records exist that inspire confidence that they reflect taxonomic diversifica-

tion sufficiently closely. But I must emphasize once more that the primary data, as summarized on the preceding and following diagrams, and discussed more in detail in Muller (1981a), directly reflect only pollen evolution, indirectly reflect adaptive trends in the reproductive sphere, and have mostly no relation to what happened in the rest of the plant body. This emphasizes once more the importance of studying the fossil pollen record, taking into account Recent evidence on form and function, and then integrating such information with macrofossil evidence.

If this is attempted, one can agree with Doyle (1978), Niklas et al. (1980), and Tiffney (1981) that neither the prejudice of Hughes (1976) against the evidence from Recent plants, nor the opinion of Heywood (1977) and Stebbins (1974) that fossil evidence is insignificant for an understanding of angiosperm evolution, will appear justified.

The evidence will be summarized on charts representing the distribution of contrasting groups of fossil pollen types. On these charts more emphasis is laid on the general evolutionary pattern within the group than on first occurrence only, which almost never coincides with origin due to the inherent deficiencies of the fossil record, even for such ubiquitous organs as pollen grains.

HAMAMELIDIDAE

In Figure 4, as in the following, Takhtajan's (1969) taxonomic concepts are followed, but it is realized that inclusion of Didymelaceae is debatable (Köhler, 1980) and that Dahlgren (1980) and Thorne (1976) have quite different concepts for this group.

The pollen types indicated are often abundant in the fossil assemblages due, of course, to the predominance of wind-pollination in many of the taxa included. Also, most of the pollen types are remarkably stable since their first appearance, no doubt because of the uniform, conservative anemophilic environment (cf. Crepet, 1979; Dilcher, 1979). *Alnus* pollen (Fig. 1a, b) is a typical representative of this group, which appears to show little evidence of co-evolution with insects. Anemophily may be responsible also for the frequent occurrence of an infragranulate exine structure.

However, it is clear that the tricolpate-reticulate members of the group shown, especially those commonly referred to as lower Hamamelididae, are underrepresented. As mentioned before, their ancestors could be present as early as



FIGURE 3. Pollen records for angiosperm orders.

the lower Cretaceous, and they may have been adapted to entomophily, since in Recent representatives like *Hamamelis* the reticulum is covered by a large amount of extremely sticky "pollenkitt" (Hesse, 1981).

The problem in the pollen morphological evolution of this group is in the transition from the tricolpate to the triporate "amentiferous" type. As already mentioned, Doyle (1969) and Wolfe et al. (1975) have suggested that the Normapolles could be transitional, but this is probable only for Betulales, Juglandales, Myricales, and Casuarinales, not for Fagales. Urticales also may have had a different origin as mentioned before.

Walker and Doyle (1975) and Wolfe et al.

(1975) have also expressed doubts whether the tricolpate, subspherical, columellate-reticulate pollen of the lower Hamamelididae could have given rise to a triangular-oblance, intragranular-smoothly tectate porate anemophilous pollen type via Normapolles. It is clear that the colporate condition, which according to Doyle (1969) has preceded Normapolles development, has been preserved in few present-day higher Hamamelididae, notably in some Fagaceae (*Castanea*, *Lithocarpus*).

However, Endress (1977) has argued for a close connection between Hamamelidales, Fagales, and Betulales and of these, only Betulales conform to the above porate amentiferous pollen type.

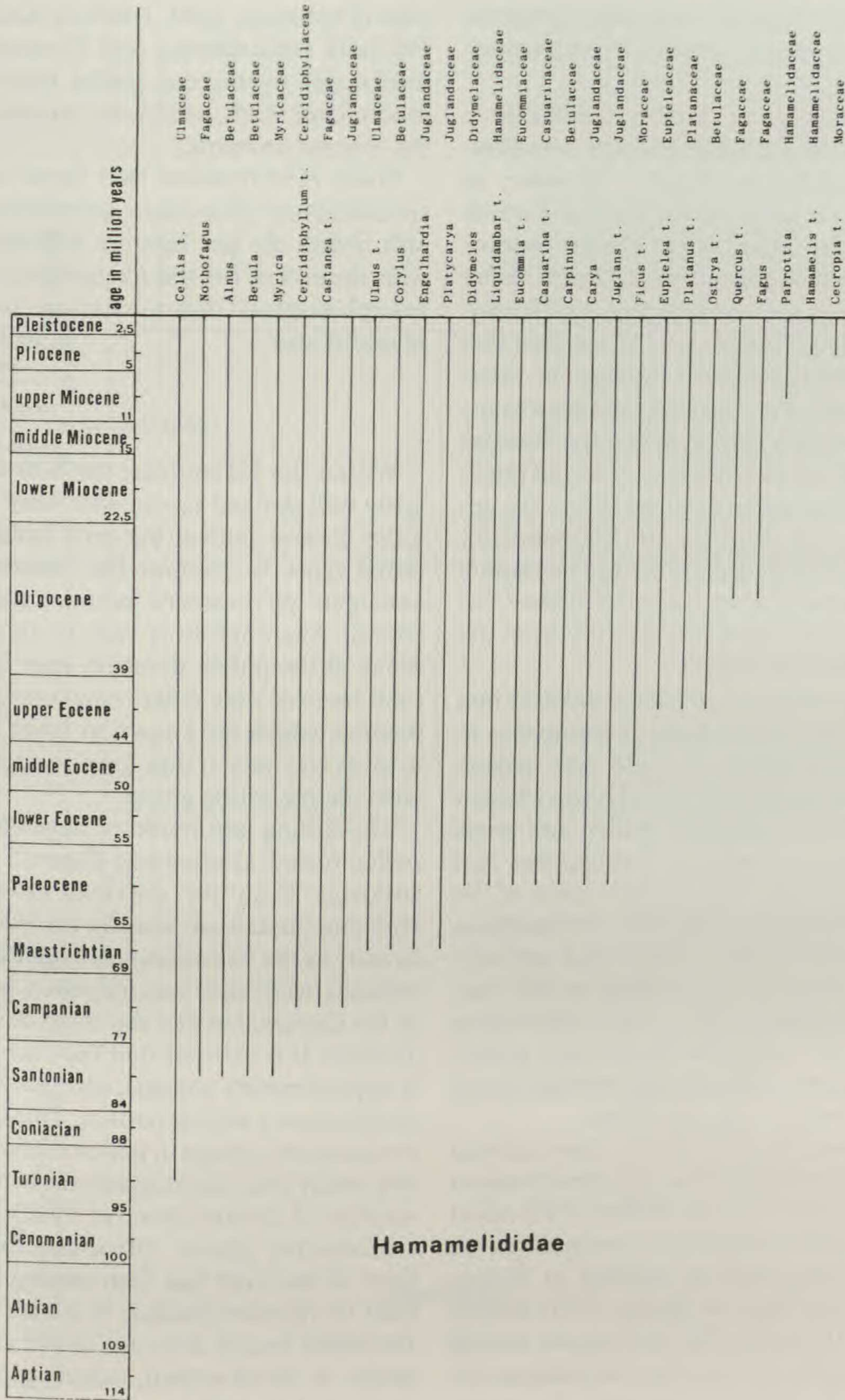


FIGURE 4. Pollen records for Hamamelididae.

Fagales, in fact, have a basically colpate-subprolate type but generally without the reticulate tectum that is so typical for lower Hamamelididae. The loss of the reticulum may be the most direct expression of the change towards anemophily. Within the Fagales, *Nothofagus* has a highly specialized, and deviating pollen type. It is thus un-

likely that Fagales went from the basic tricolpate-reticulate type through a Normapolles stage to the Recent types. Rather, a *Castanea* pollen type may be placed at the base. Some of the genera that produce this pollen type, such as *Lithocarpus* and *Castanopsis*, have retained some entomophilous characters; and the pollen type that

retains traces of columellar-reticulate structure at the poles is remarkably similar to certain mid-Cretaceous types.

Therefore, it is of great interest that Wolfe et al. (1975) claim, on the basis of foliar morphology, that Juglandales are allied to Rosidae, in which the colporate type is dominant and in which anemophily is rare. Because the closest connection between Normapolles and a Recent taxon is with Juglandales and not with Fagales (Skarby, 1968; Wolfe, 1973; Nichols, 1973), the idea that the Normapolles-Juglandales lineage is intermediate between the Fagales/Betulales/Myricales/Casuarinales on one hand and the Rosidae on the other may seem attractive. It would imply a lower Cretaceous differentiation before the appearance of the first Rosidae and Hamamelididae from the Turonian, and probably even before the first appearance of Normapolles in the Cenomanian. A similar view has recently been expressed by Cronquist (1981).

As already stated, it is considered unlikely that Urticales have developed from Normapolles in view of the early record of *Celtis* type pollen, although Walker and Doyle (1975) judge *Planera* (Ulmaceae) to have colporate pollen and stress the presence of arci both in Normapolles and Ulmaceae. It is likely that further study of the fossil pollen record and especially of transitions between types will provide important new evidence to help solve these questions. In this connection Zavada and Crepet's (1981) description of middle Eocene celtidoid flowers and pollen, which suggest a transitional stage between insect and wind pollination, are significant.

Regarding macrofossil evidence, there is broad agreement in the timing of the early development of at least some major groups. Ruffle (1980) raised the possibility that certain leaf remains from the lower Cretaceous could be referred to Hamamelidales (cf. also Doyle & Hickey, 1976; Hickey & Doyle, 1977), whereas the well known records of *Platanus*-like leaves from the Cenomanian onwards could be said to agree with the regular occurrence of tricolpate-reticulate type pollen in this period.

Fagaceae appear to have roots in the cenomanian, although in general Cretaceous representatives had leaves that deviated considerably from the Tertiary ones; whereas, by the middle Eocene, the family appears to have diversified strongly (Crepet, 1979). *Betula* leaves from the Santonian and betulaceous wood from the Campanian agree remarkably well with the earliest pollen records, which are from the lower Seno-

nian (Cronquist, 1981; Ruffle & Knappe, 1977). For both Juglandaceae and Ulmaceae, the earliest upper Cretaceous pollen records antedate macrofossil finds, which are known only from the Eocene onwards.

Wolfe (1973) stated that forms showing the specialization of modern amentiferous families and orders do not become differentiated until near the end of the late Cretaceous, when pollen morphological differentiation is very pronounced also.

MALVANAEE

Within the Dilleniidae, the Malvanae form a fairly well defined taxon, with very morphologically diverse pollen, but with sufficient transitional types to confirm the coherence, and to anticipate phylogenetic junctions, in the fossil record. Anemophily is rare in this group and much of the pollen diversity may have a structural basis or may reflect co-evolution with pollinators, which are known to range from insects to birds and bats. It thus forms a striking contrast with the preceding group.

The timing and mode of development of the pollen record as shown in Figure 5 differ rather strikingly from the previous group. Whereas Hamamelididae are already recorded by pollen as early as the Turonian and even earlier as macrofossils, Malvanae can, on pollen, be traced only to the Campanian and the main development is Tertiary. It is obvious that the cumulative curve is approximately straight, and that all orders included show a similar pattern. This indicates that evolutionary change in pollen characters went on at a steady rate, and suggests the action of a large number of diverse selective forces acting in the reproductive sphere. Obviously the stabilizing force of the wind has been lacking here, in contrast to Hamamelididae. It is also curious that the pollen record does not detect an early, slow phase of development, which presumably remains undetected because of uncharacteristic ancestral pollen types.

According to Walker and Doyle (1975), Elaeocarpaceae are rather primitive in Malvales and have a small, tricolporate, smooth pollen type that could be considered ancestral. Also, the fossil pollen record of Euphorbiaceae is clearly biased towards the more specialized types. Only for Bombacaceae has Wolfe et al. (1975) found evidence for a relatively unspecialized type from which the highly specialized Tertiary pollen types can be derived.

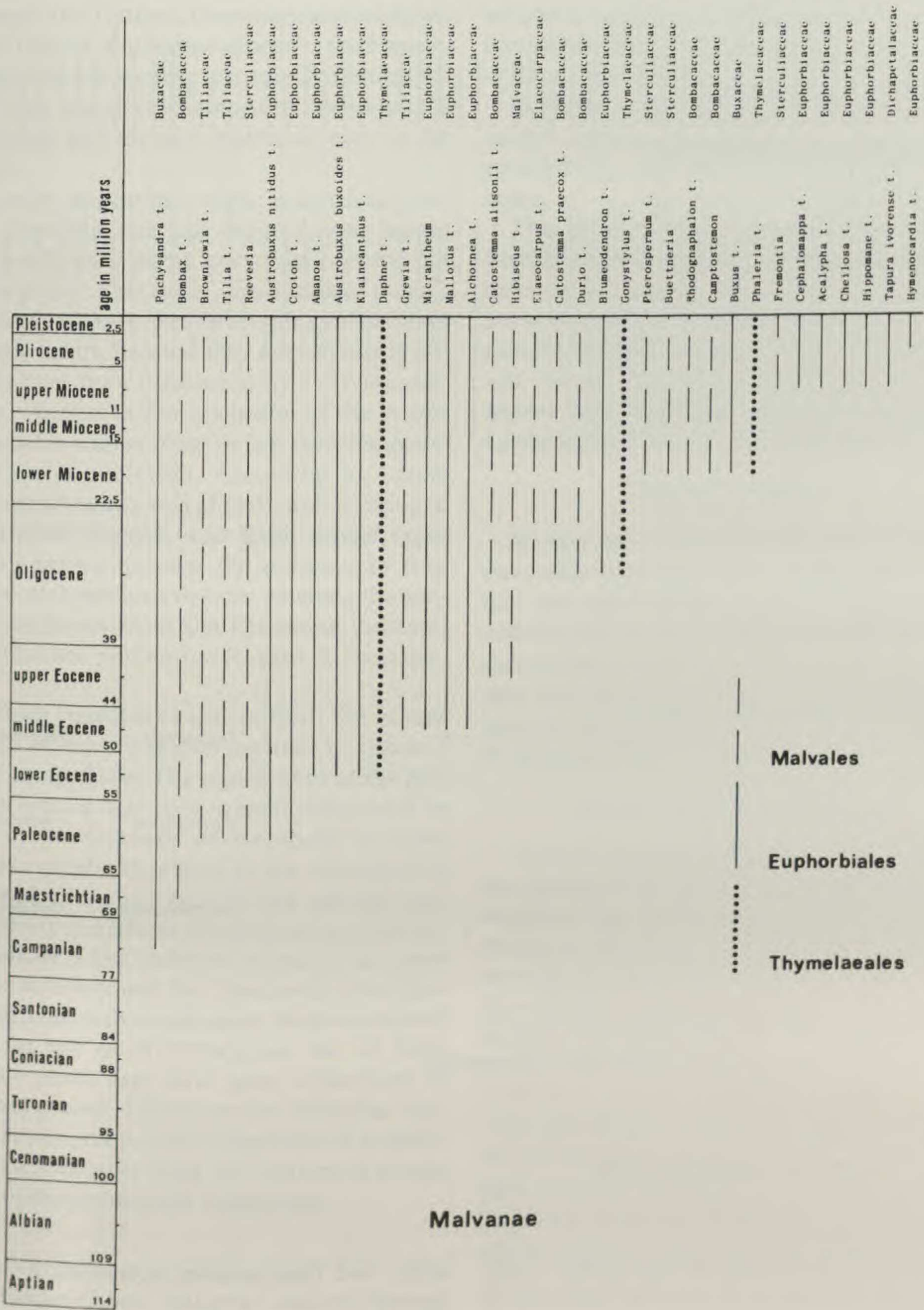


FIGURE 5. Pollen records for Malvanae.

The macrofossil record for Sterculiaceae starts earlier than the pollen record but is mainly based on leaves from the Cretaceous. Macrofossils of Tiliaceae, Malvaceae, Bombacaceae, and Euphorbiaceae, however, start appearing only in the Tertiary, in line with the microfossil evidence. Thus, as a whole the macrofossil record appears to be synchronous with the microfossil record, confirming that the pollen data as summarized

in Figure 5 do reflect the general evolutionary radiation of Malvanae.

ASTERIDAE

Figure 6 shows the pollen record for Asteridae, a taxon which is more or less equivalent to the "tubiflorae" of an older generation of angiosperm systems, such as Wettstein's. The pollen

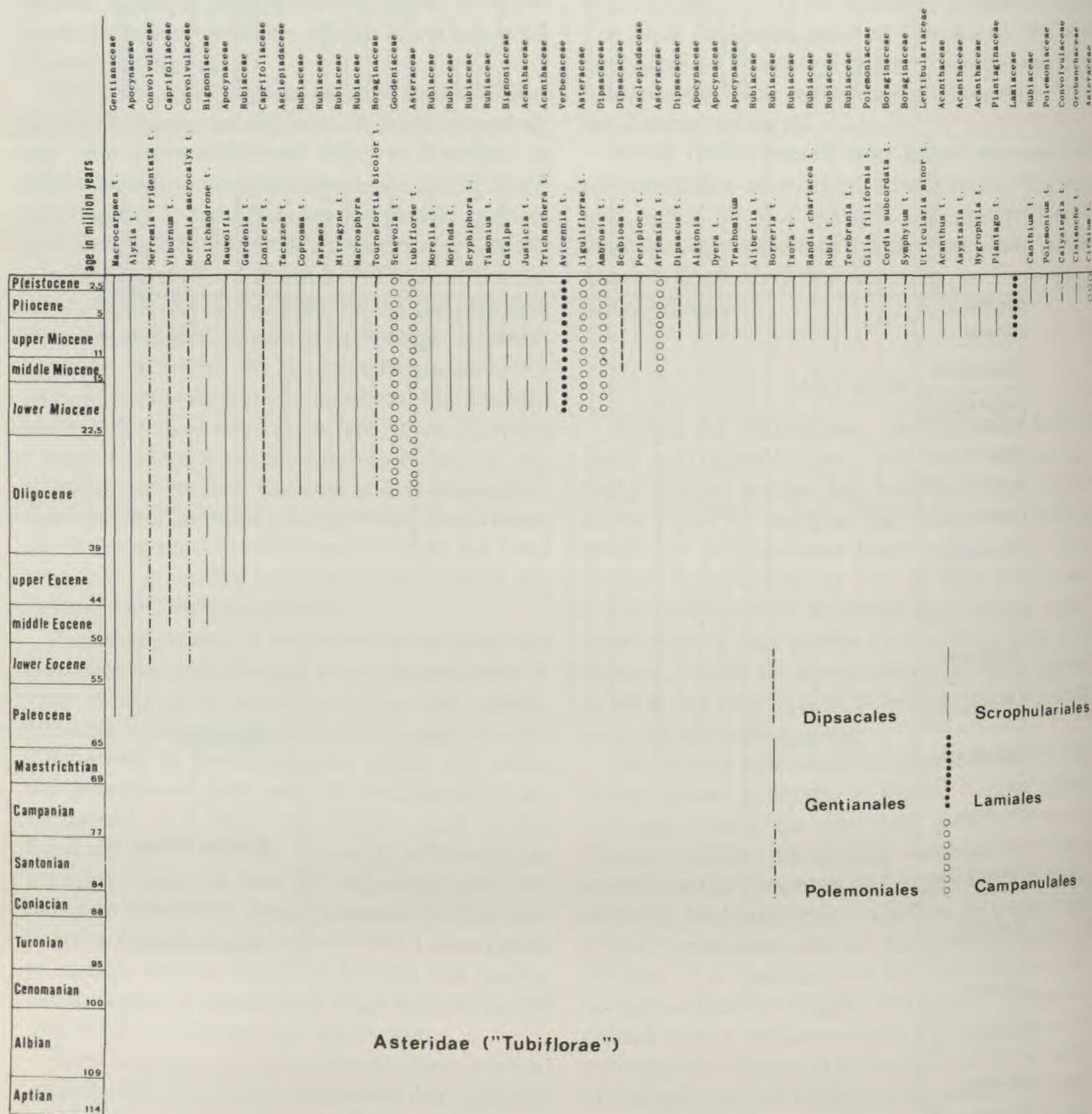


FIGURE 6. Pollen records for Asteridae.

morphological evolution in this group starts slowly in the Paleogene, accelerates markedly in the Neogene, and is probably continuing today. This clearly reflects active evolution in the reproductive sphere, and there seems to be little doubt that it indicates a process of co-evolution with long-tongued insects, although pollen/stigma interactions, germinating efficiency, and harmonomegathy may also have been important. Especially in Asteraceae, the latter factor may have been dominant (Bolick, 1981).

There appears to be some difference in timing of main development, with Dipsacales, Gentia-

nales, and Polemoniales appearing earlier than Scrophulariales, Lamiales, and Campanulales.

Macrofossil evidence partly supports the timing suggested by the pollen record, although Caprifoliaceae and Apocynaceae are known from the Cretaceous already.

The presence of Gentianaceae in the Paleocene has recently been documented by Crepet and Daghljan (1981) based on funnel shaped flower remains containing *Pistillipollenites macgregorii* pollen, which is comparable to pollen of the Recent genus *Macroparva*. This record was not quoted in Muller (1981). Caprifoliaceae become

abundant in the Tertiary, Boraginaceae are known from the Eocene, Rubiaceae appear in the Eocene, and Bignoniaceae are first recorded from the Oligocene. The macrofossil record of Asteraceae is very limited and appears restricted also to the Tertiary.

The earlier appearance in the macrofossil record of Caprifoliaceae and Apocynaceae agrees with the difference in the microfossil record but is out of phase. This again may indicate mosaic evolution, leaf characters developing earlier than pollen characters, because they are obviously not likely to have been influenced by evolving pollinators, whereas flower evolution in the Asteridae probably started more or less simultaneously with insect evolution. According to Crepet (1979), entomophily was already well developed in the middle Eocene, and fossil flower types from this period indicate the presence of four orders of anthophilous insects, whereas the gentianaceous flower from the Paleocene indicates even earlier bee pollination (Crepet & Daghljan, 1981).

The three cumulative curves from the groups discussed before are shown together in Figure 7 for easy comparison. The significance of the pollen data here is that they suggest differences in timing of evolutionary development in those character complexes related to the reproductive sphere and, in a more general and indirect way, differences in taxonomic diversification. For Hamamelididae, a fast, tachytelic phase in the upper Cretaceous is followed by a bradytelic one characterized by slow diversification. Malvaceae show a constant rate of diversification, but an early tachytelic phase may have gone undetected in the pollen record. The curve for Asteridae suggests that this group is still essentially in a tachytelic phase, adapting since the Tertiary to a large variety of environmental conditions.

LEGUMINOSAE (FABALES)

Figure 8 shows the contrasting records for the three main groups of Leguminosae. Caesalpiniaceae appear as the oldest, with a strongly diversified number of pollen types. Macrofossils from the Maestrichtian confirm the earliest occurrence of pollen for this taxon.

Mimosaceae are recognizable as soon as their characteristic polyads appear in the middle Eocene, and tetrad pollen has been found associated with mimosoid flowers from the same period (Crepet & Dilcher, 1977) indicating a phase

of active evolution in flower structure. An earlier tricolpate phase of single grains may have gone undetected, however.

Fabaceae are nearly absent in the fossil pollen record, presumably because of the low pollen productivity and lack of characteristic pollen types.

This picture broadly agrees with Raven and Polhill's (1981) views on the development of the legumes as a whole. They assume a Cretaceous development for Caesalpiniaceae with a Paleogene radiation of the main branches of the tropical, woody legumes (Caesalpiniaceae, Mimosaceae, and Fabaceae) and a proliferation of advanced Fabaceae in the Neogene is postulated.

MONOCOTYLEDONS

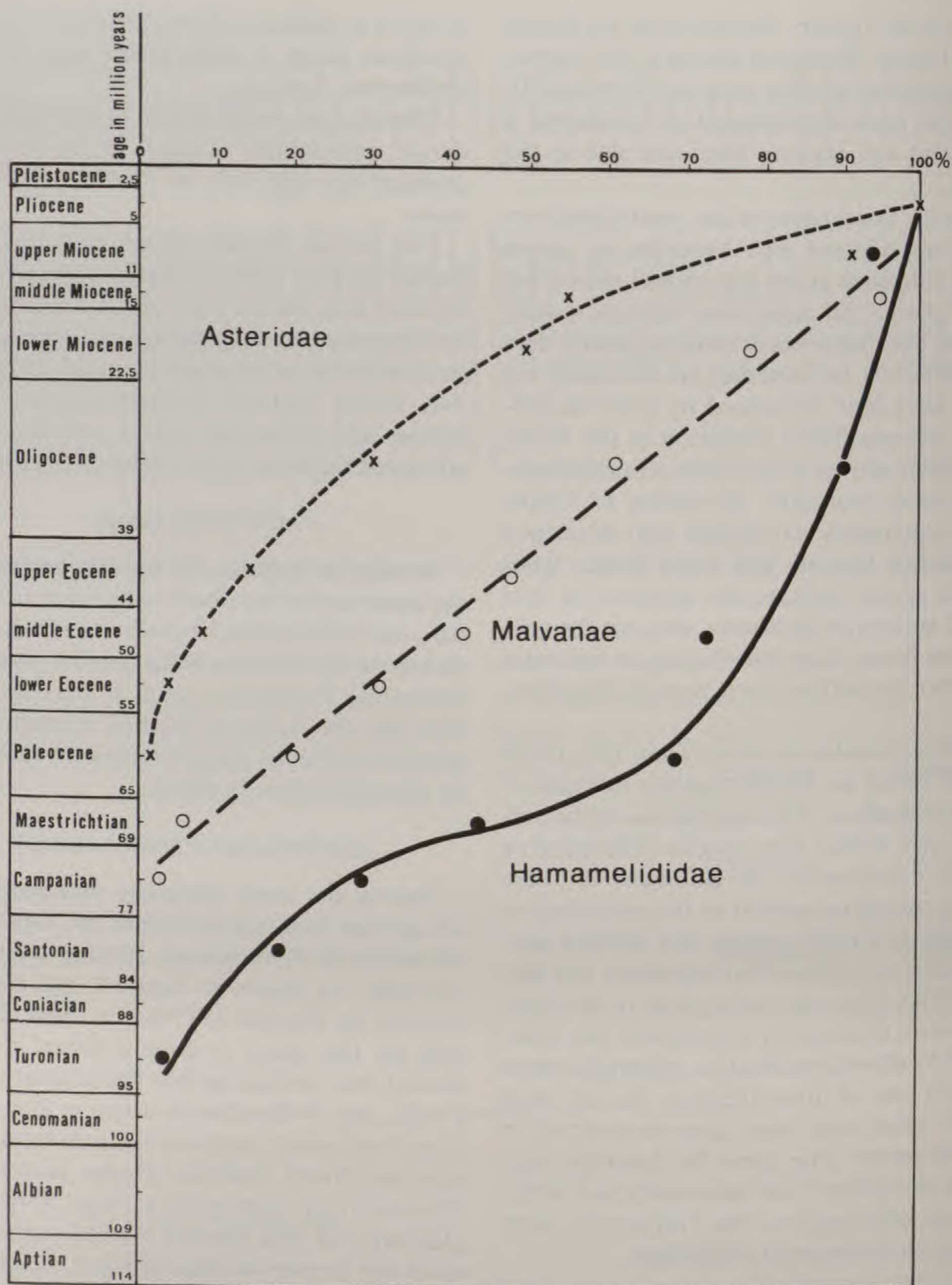
As may be recalled, the first monocotyledonous pollen types have been recognized in the Aptian, but these cannot be more closely identified, and the same difficulty holds true for most of the succeeding Cretaceous types. It may be significant that the pollen of the first modern groups appears only in the upper Cretaceous, as will now be discussed more in detail.

RESTIONACEAE (COMMELINIDAE)

Among the most intriguing monocotyledonous groups well represented in the fossil pollen record are the Restionaceae, starting in the Maestrichtian. As shown in Figure 9 and discussed recently by Hochuli (1979), the fossil distribution for this taxon is quite different from the Recent one, indicating that the present range is a relict one. A Gondwana origin is likely, however, from which extensions northwards to Europe and North America became possible. The Maestrichtian occurrence in West Africa, coupled with the total absence of restionaceous pollen in the Tertiary of tropical South America and India, indicates that migration northwards took place via Africa. Hochuli (1979) has suggested that *Rhizocaulon*, a macrofossil occurring in the Upper Cretaceous and Tertiary of western Europe, may be related to Restionaceae, but this plant shows rather profound points of difference with the Recent genera of this family, and its pollen has not yet been isolated from its fructifications.

POACEAE (GRAMINEAE)

The first, rather doubtful, fossil grass pollen grains appear in the Campanian. They are scarce



Pollen morphological differentiation, cumulative % curves

FIGURE 7. Cumulative % curves for Hamamelididae (dots), Malvanae (circles), and Asteridae (crosses).

and badly preserved. Firm records date from the Paleocene and they become increasingly abundant in the course of the Tertiary.

Although macrofossil remains of this family have been described already from the Cretaceous, firm records based on caryopses date only from the Lower Eocene (Daghlian, 1982). This confirms the impression that the main development of the family started only in the earliest

Tertiary. Its pollen record, however, partly will reflect the adaptation towards anemophily (cf. Takhtajan, 1969: 238).

CYPERACEAE

The characteristic pollen grains of this family are first found in the Middle Eocene and this agrees well with the macrofossil record, which starts with fruits in the Lower Eocene of England.

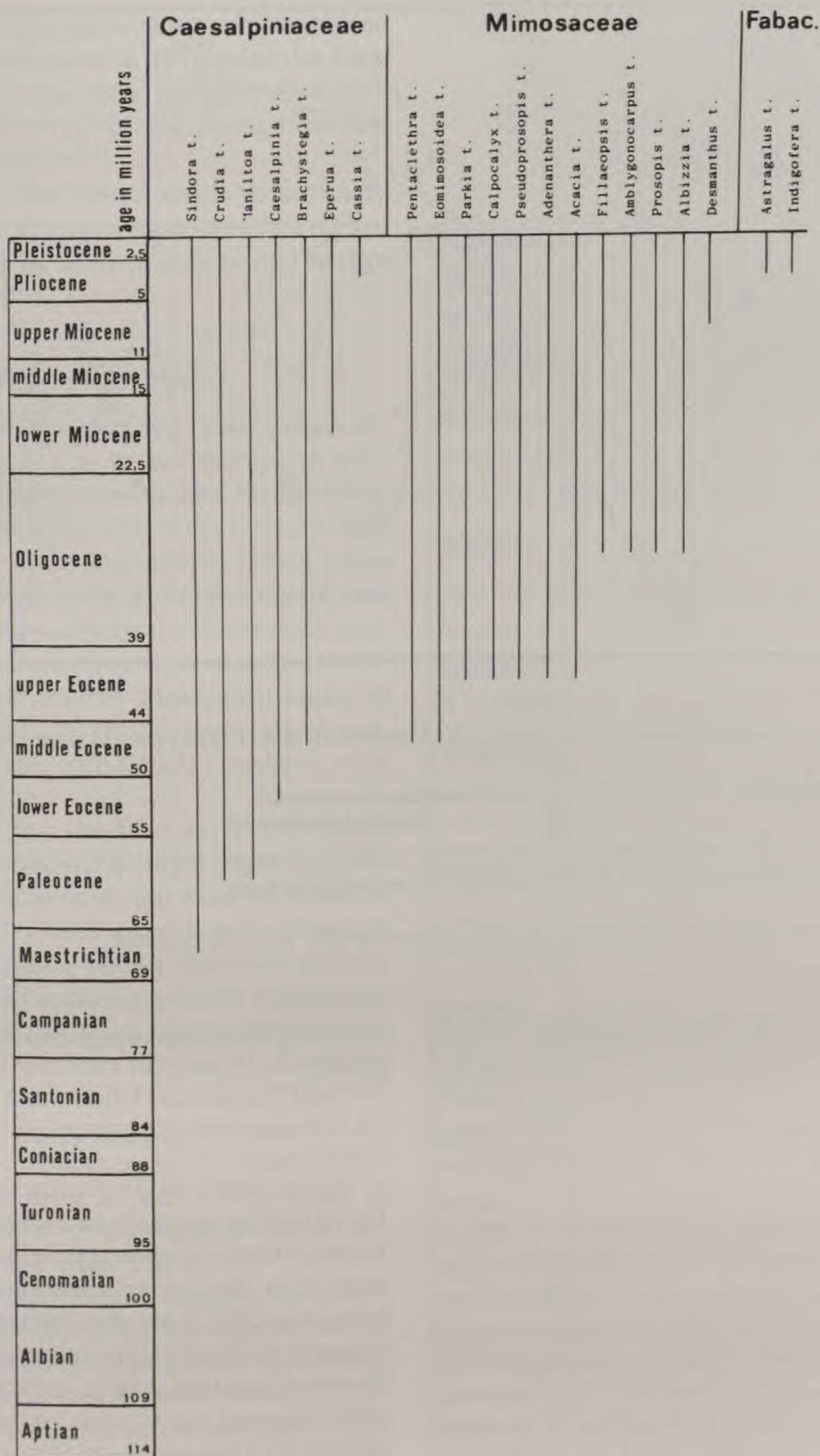


FIGURE 8. Pollen records for Fabales.

Earlier macrofossil records of Cyperaceae are considered dubious (cf. Daghljan, 1981).

ARECACEAE (PALMAE) (ARECIDAE)

Whereas the preceding monocotyledonous families each had a fairly uniform pollen type, Palmae are much more diversified in this respect.

The distribution of the recorded types is shown in Figure 10. Again, the more characteristic lepidocaryoid types dominate here, but taking other, less clearly identifiable types into account, the microfossil record suggests a lower Senonian diversification phase in West Gondwanaland, and a second diversification in Southeast Asia must

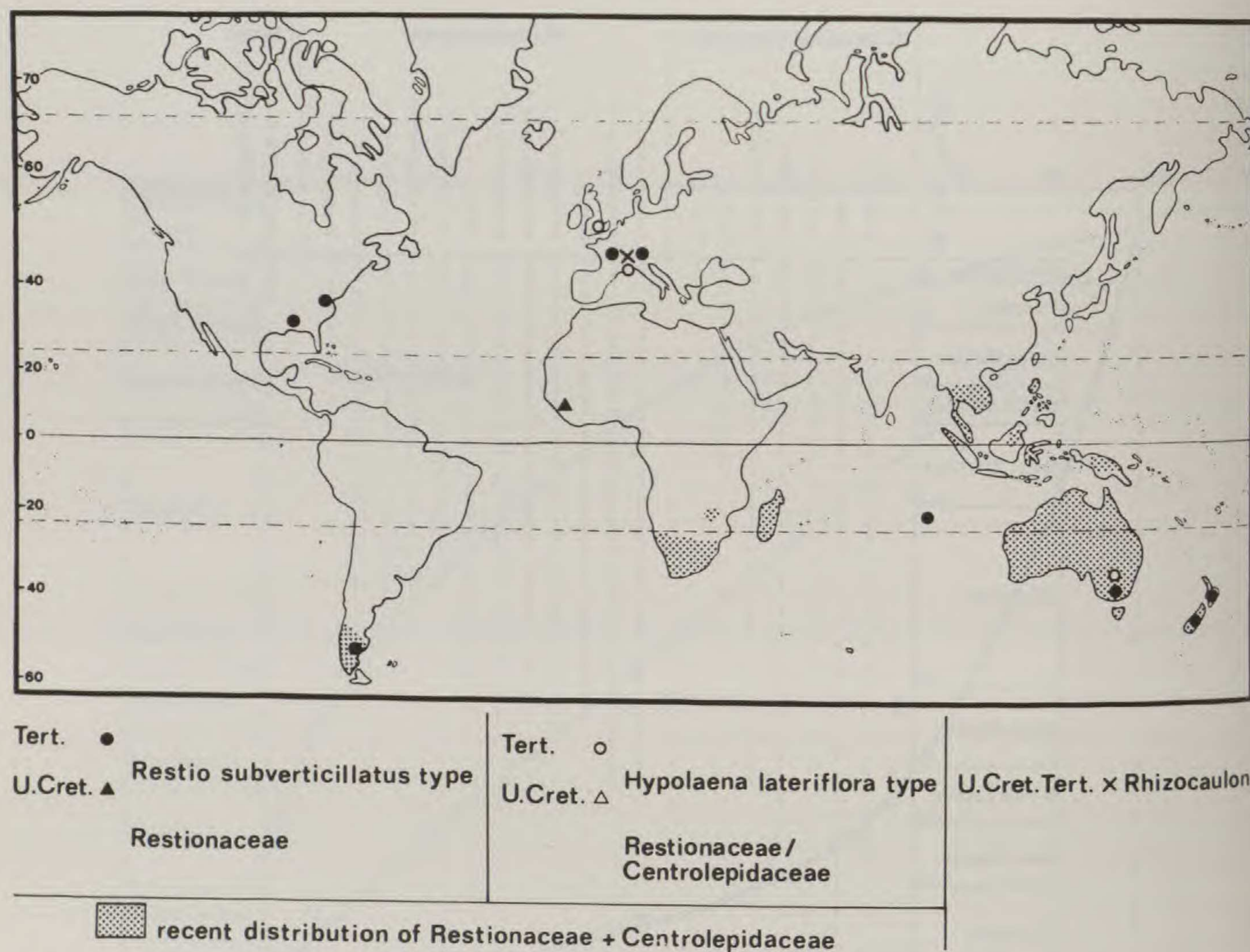


FIGURE 9. Recent and fossil distribution of Restionaceae and Centrolepidaceae.

have taken place in the Tertiary (Muller, 1979b). The macrofossil record supports this picture because fossil palm wood starts appearing regularly in the Senonian, and both leaves and stems occur in the Santonian of North America (Daghlian, 1981).

A Gondwana origin is postulated by Moore (1973) and Dransfield (1981) on the basis of Recent distribution patterns and a revised taxonomy. It is not at all clear what factors have caused this relatively late development, although an obviously secondary development of the only major woody group of monocotyledons, from semi-aquatic herbaceous ancestors in the Lower Cretaceous, which has taken considerable time to achieve, is indicated.

PANDANALES

According to the pollen records, this group starts occurring in the Maestrichtian, although fossil fruits have been described from the Lower Eocene of India. These, however, are not certain

to belong to Pandanaceae according to Daghljan (1981).

TYPHALES

Tetrad pollen of Typhaceae is recorded from the Paleocene onwards and single grains that can belong either to Typhaceae or Sparganiaceae also date from this period. Sparganium fruits have been described from the Paleocene, while macrofossils of *Typha* have been recorded from the Eocene (Daghlian, 1981), indicating good agreement between micro- and macrofossils and suggesting a Paleocene development of the family.

Looking back on the monocotyledonous record as a whole, one can dimly discern the presence, already in the Lower Cretaceous, of an older branch represented by vaguely identifiable types which probably have been produced by ancestral Alismidae and Liliidae, while somewhat later, in the Upper Cretaceous, firmer evidence for the development of Commelinidae and Arecidae appears.

The relatively late appearance of Gramineae and Cyperaceae supports in particular the view of Stebbins (1974) that these families are highly advanced and actively evolving young branches of the monocotyledons.

It is, however, clear that a much closer study of the Cretaceous macro- and microfossil record will be necessary to confirm this tentative picture.

EVOLUTIONARY MODEL

So far, we have discussed large scale taxonomic diversification. It may be worthwhile to consider smaller scale phenomena also, because here we may have a chance to detect the evolutionary process at work. Most angiosperm pollen types appear fairly sudden in the geological record and that clearly transitional series, even in thick sedimentary sequences known to be nearly continuous, such as the Eocene Maracaibo basin in Western Venezuela or the Neogene northwest Borneo geosyncline, with which I happen to be familiar, are scarce.

To generalize too much about evolutionary processes on the basis of a single organ, i.e., the pollen grain, is dangerous; but because pollen is involved in the critical reproductive phase of fertilization and clearly shows abundant shifts in a suitable series of sediments, some worthwhile facts may emerge. Will we find a situation reflecting Darwin's view of a myriad intermediates or a sequence of punctuated equilibria? The lack of intermediates in macropalaeobotany has recently been commented upon by Stidd (1981: 96-97), and evolution in plants is as likely to proceed via punctuated equilibria as it is in animals (Gould & Eldredge, 1977).

In theory, an equilibrium situation in pollen characters may be disturbed without the rest of the plant being affected, except that the overall efficiency and competitive power (level of adaptation) may change for better or worse, either intraspecifically leading to population shift or interspecifically causing competition followed by replacement and extinction. Three different cases will be discussed.

1. *Santalales*. It has been argued that the extinct group of plants that produced *Aquilapollenites* type pollen, and that was common in the upper Cretaceous of part of the northern hemisphere, was related to Santalales based on its resemblance to certain present-day loranthaceous and santalaceous pollen types (Jarzen, 1977).

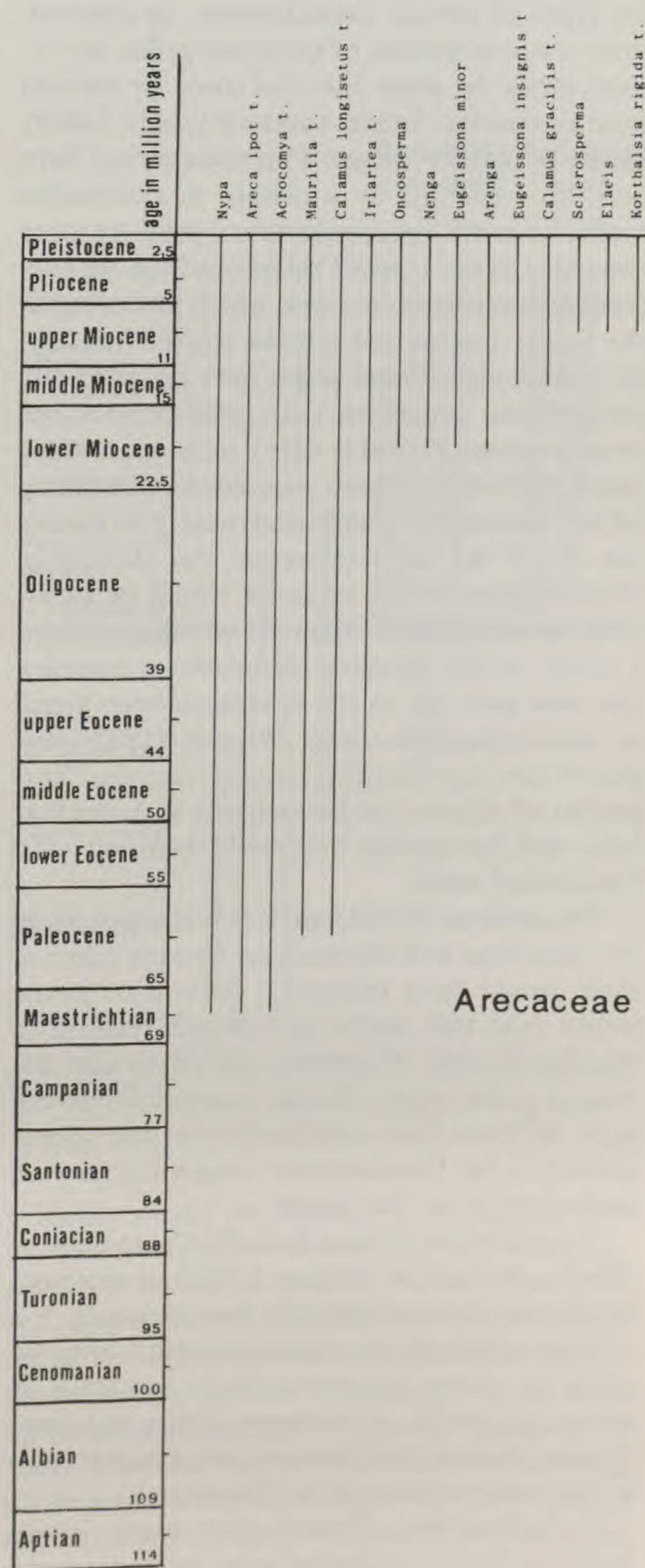


FIGURE 10. Pollen records for Arecaceae.

ceous and santalaceous pollen types (Jarzen, 1977).

By comparison with Recent harmomegathic types, the peculiar morphology of this genus can be described as a multidimensional harmomegathic stress system. The oblate, disc-shaped pol-

len types of certain Lorantheae, in contrast, show a concentration of harmomegathic movement along the polar axis and could be derived from an *Aquilapollenites* ancestral type by a fairly simple structural change. This change may have been accompanied by a change in pollination mode, since the *Aquilapollenites* types were more abundant in the Upper Cretaceous than the succeeding lorantheaceous types, which first occur in the Lower Eocene but remain scarce. Actually, the crucial transitional stages have not been discovered yet, suggesting that small populations were involved. Probably only a minor part of the *Aquilapollenites* complex succeeded in branching off in a new adaptive niche and most of its species die out of the top Cretaceous. An alternative interpretation of the evidence would be to assume an independent origin of Lorantheae from a much earlier ancestral santalaceous complex that also gave rise to the *Aquilapollenites* group in mid-Cretaceous times. Wiggins (1982) suggested that *Expressipollis striatus* from the Campanian of Alaska can be assigned to Lorantheae, and this species thus could form part of a transitional series.

This separate development is even more likely for Olacaceae and Santalaceae, because some of their genera have retained a basic tricolporate pollen type that shows no obvious relation to *Aquilapollenites*. Moreover, in Olacaceae advanced pollen types, like the *Anacolosia* type are quite different from *Aquilapollenites* and appear already in the Maestrichtian, suggesting an even earlier origin for this family.

Anacolosidites striatus from the Campanian of Alaska, claimed by Wiggins (1982) to represent Olacaceae, is more probably lorantheaceous.

Thus, although the *Aquilapollenites* complex could be placed taxonomically in Santalales as an extinct family, with closest affinity to Lorantheae, its exact phylogenetic relationship within the order remains to be discovered.

2. *Juglandales*. Rather more firmly established is the connection between *Juglandales* and the preceding Normapolles group, the morphological link between which has already been discussed in a previous paragraph. As in the preceding case, most Normapolles plants became extinct, some as late as Eocene, but a few appear to have given rise, by abandonment of the highly specialized apertural adaptations typical for the group, to a new line of evolution. Nichols (1973) has studied these early *Juglandales* in detail and it appears here also that the transitional popu-

lations may have been small. The subsequent evolution leading towards pollen types such as those of *Engelhardia*, *Carya*, *Platycarya*, and *Pterocarya* can, however, be followed in great detail and appears to be quite gradual, making it difficult to establish precise taxonomic separations. Structurally, these later pollen types do not diverge strongly and all remain typical wind-pollinated forms. Taxonomically the Normapolles group can be recognized as an extinct family within *Juglandales*.

3. *Sonneratia*. On a much smaller scale is the origin of the genus *Sonneratia*. As shown in Figure 11, two Recent pollen types, which are restricted to two good species that hybridize but produce infertile offspring, were found to originate via a short-lived phase of small transitional populations, from an extinct ancestral type resembling certain lythraceous pollen types (Muller, 1978). This diagram clearly shows the typical branching pattern of the punctuated equilibrium model of Eldredge and Gould (1972).

The critical transition of the pollen characters involves a short period of morphological reconstruction that can be interpreted as a rearrangement of the harmomegathic stress system (Muller, 1981b). The striking subsequent increase in abundance testifies to the ecologic success of the new taxa, which presumably competed directly with the less specialized parent plant. However, what other factors have been involved remains quite unknown in the absence of macrofossils.

As far as pollen characters are concerned, the evolutionary process has still not stabilized itself, as witnessed by a large degree of morphological variability still present, and the hybridization between several species of the genus (Muller, 1969; Muller & Hou-Liu, 1966).

The early ancestors of this complex may have been plants from the Tethys shores, adapted to insect pollination, although *Sonneratia* is now adapted to pollination by fruit-eating bats, which appear in the fossil record about at the same time as the first pollen records (Muller, 1978).

The critical factor for this evolutionary development is, of course, reproductive isolation. Pollen variability, as present in the Recent species of *Sonneratia*, in itself does not promote isolation except when crosses tend to increase pollen infertility. The changes anticipated in some of the Recent populations of *S. alba* and *S. caseolaris* could conceivably lead to another new species in this way, but to be evolutionarily successful, the new species has to change its ecology

also, in order to invade a new niche or to replace its parent, as probably happened in the early Miocene.

The lesson from this is that pollen development, in addition to seed and embryo development, is closely related to the coming into existence of reproductive isolation, much more probably than wood or leaf characters. After all, a cross between two leaf types almost always will result in a new leaf shape, which must be of about equal efficiency as the parent leaves, but cannot influence reproductive isolation, except very indirectly if a shift in niche results. Taxonomically, the pre-Miocene taxa appear to be intermediate between Lythraceae and Sonneratiaceae and may represent a distinct genus, ancestral to the younger species of *Sonneratia*.

When these three examples are compared, it will be clear that, for obvious reasons, the most detailed evidence has been obtained for a group of mangrove taxa; but Juglandaceae may have evolved in or close to a river floodplain and thus also have left a fairly continuous record. For the Santalales complex, evolution may have taken place far from depositional areas, however. This confirms Axelrod's (1970) claim that only in cases where evolution takes place close to the coast can the process itself be detected.

All cases agree in that they appear to follow the punctuated equilibrium model in showing evidence for small transitional populations, followed by more gradual evolutionary change. They also agree in the presence of extinct ancestral complexes that link younger descendants.

Obviously, a similar process could be postulated for the earliest evolution of the angiosperms as a whole.

AGE AND ADVANCEMENT INDEX

In the preceding discussion the fossil pollen record was compared with the taxonomic subdivision of Takhtajan (1969), but taxonomic subdivisions are subjective, especially at higher levels and many different systems exist.

A more objective approach is to compare directly with the character complexes of the taxa, and for this purpose Sporne's (1982) advancement index (A.I.) of dicotyledonous families is available, in which a low index would indicate families that have retained a high proportion of 'primitive' character states. A cardinal difficulty in Sporne's approach has always been the danger of circular reasoning and any support from fossil

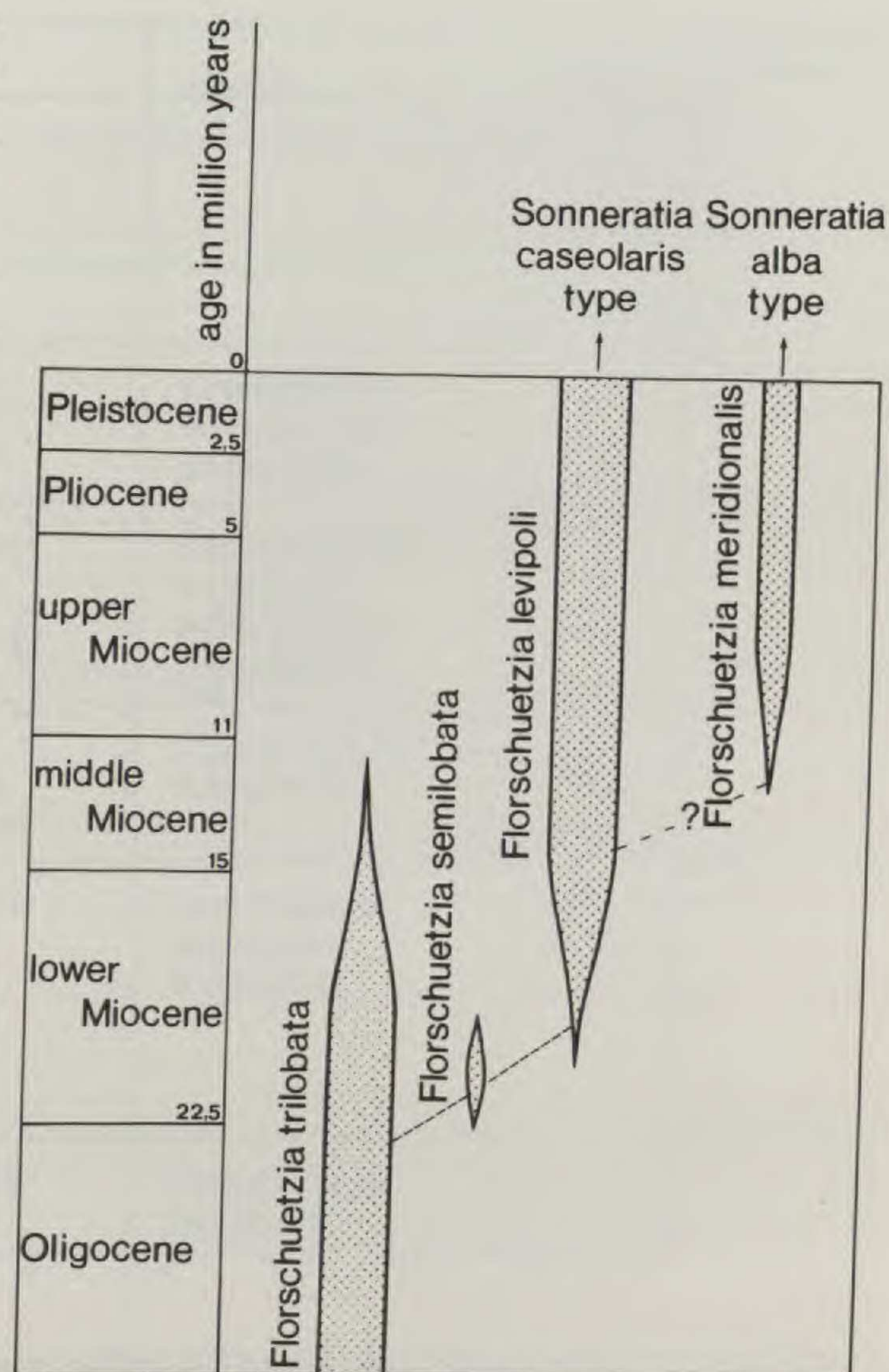


FIGURE 11. Pollen records for Sonneratiaceae in West Malesia.

evidence would be decisive in testing the prediction that families with a high A.I. would appear later in the record than those with a low A.I. Sporne (1980) himself had already tested the earlier data published in 1976 and found that the prediction could be confirmed. On the basis of the present data and of Sporne's latest list of 1980, I retested the prediction and the resulting scattergram is shown in Figure 12. Obviously, a large amount of scatter is present, which is no doubt due to a number of disturbing factors: entomophilous taxa will be recorded later than anemophilous ones, coastal species tend to be recorded earlier than inland species, and families that contain both unspecialized and advanced pollen types tend to be recorded only when the latter have evolved. Nevertheless, the expected correlation, if weak ($r = -0.3$), is there and highly significant ($P > 0.95$). If we look at the averages for certain periods we can see that they are situated approximately on a straight line.

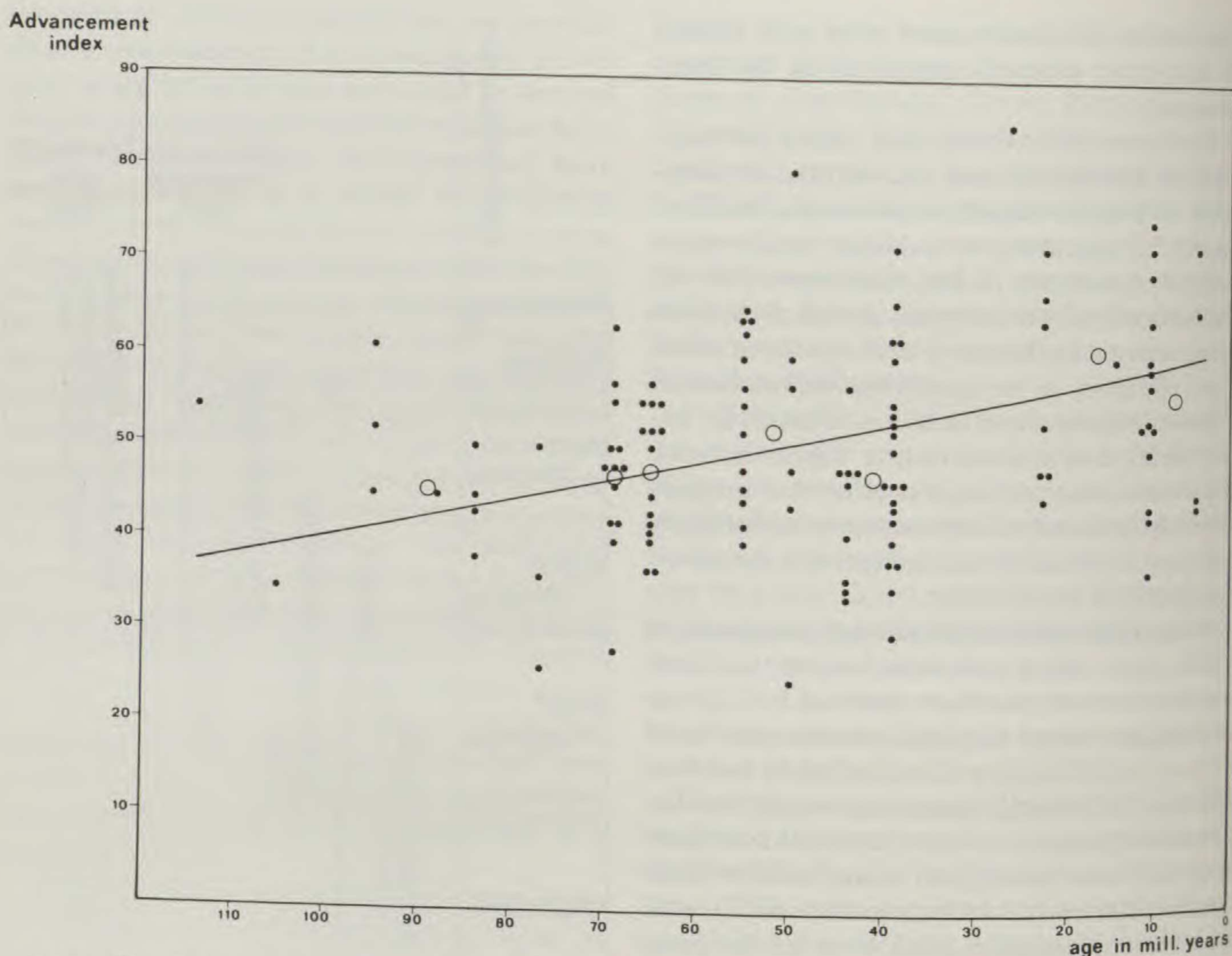


FIGURE 12. Relation between age of first pollen record and Sporne's advancement index for dicotyledonous families. Pearson's product-moment correlation $r^2 = -0.3$; $P < 0.05$, $df = 116$. Data based on Muller (1981) with the addition of Gentianaceae—Paleocene (Crepet & Daghljan, 1981) and a change of Winteraceae from Maestrichtian to Aptian/Albian (Walker et al., 1983).

Perhaps the results become more meaningful in Figure 13, which shows the relation between A.I. and first occurrence for about 52 selected families. For these families, the pollen record is exceptionally reliable or extensive.

It may be noted that, if Sonneratiaceae are merged with Lythraceae, the correlation improves. In fact, the difference in A.I. between these two closely related families is very much influenced by the woody character of the former and the many advanced herbs in the latter.

Most striking is the contrast between the Cretaceous plus Paleocene and the post-Paleocene families, but clearly families like Winteraceae and Schisandraceae are prime examples of families with a low A.I., which can only be detected when their specialized pollen types appear. Magnoliaceae, as stated before (Muller, 1970) are probably completely underrepresented and, were it not for the significant ancestral chloranthaceous and winteraceous grains in the lower Cre-

taceous, our survey would hardly have produced any significant information on the earliest phase of angiosperm development at all.

One can also test which of the character complexes used by Sporne (1980) show the closest correlation with age of first pollen record. This has been attempted by Baas (1982) for xylem characters. He comes to the conclusion that families recorded from the Cretaceous show a higher incidence of primitive vessel, fiber, and parenchyma features than those that appear in the Tertiary, thus confirming the well-known "Baileyan trends" in xylem evolution.

The apparent straight line relation between age of first occurrence and A.I., if extrapolated, strongly suggests a Jurassic 'origin' for the angiosperms as a whole. This can also be tested in a different way, by plotting the time of first appearance on the diagram, published by Stebbins (1974, fig. 11-1), based on Cronquist (1968), which includes the monocotyledons and also ar-

Advancement Index	Cretaceous	Paleocene	Eocene	Oligocene–Pliocene
71–75				Acanthaceae Compositae
66–70				Plantaginaceae
61–65	Chenopod./ Amaranth. Haloragaceae		Loranthaceae Nyctaginaceae Santalaceae	
56–60	Proteaceae	Apocynaceae	Convolvulaceae Lythraceae Malpighiaceae Umbelliferae	
51–55	Onagraceae Chloranthaceae Ulmaceae	Icacinaceae Polygalaceae Anacardiaceae	Thymelaeaceae Alangiaceae	
46–50	Juglandaceae Myricaceae Sapotaceae Leguminosae Symplocaceae Olacaceae	Casuarinaceae	Lecythidaceae Malvaceae Rubiaceae	Sonneratiaceae Trapaceae
41–45	Aquifoliaceae Myrtaceae Sapindaceae Fagaceae Bombacaceae Ericac./Clethrac.	Didymelaceae Tiliaceae	Caryocaraceae Guttiferae	
36–40	Annonaceae Betulaceae Buxaceae	Euphorbiaceae Hamamelidaceae	Rhizophoraceae	
31–35	Winteraceae			
26–30	Schisandraceae			

FIGURE 13. Age of first pollen record and Sporne's advancement index for selected families.

ranges the families according to their relative advancement, estimated differently from Sporne, however. Here also, Asteridae stand out as the youngest and most advanced angiosperms. As is well known, this group also has the highest proportion of herbaceous types within the dicotyledons, supporting the notion, first formulated by Sinnott and Bailey (1914) nearly 70 years ago, that, in general, woodiness is primitive and herbaceous growth habit advanced within dicotyledons. Note, however, that within the monocotyledons the woody palms appear young and were probably derived from herbaceous or shrubby ancestors, as also postulated already by these same authors.

As in the correlation diagram shown previously, this diagram also shows the central hole of very low A.I., through which, metaphorically speaking, the earliest angiosperms have emerged undetected as yet by any pollen or macrofossil record and not having survived unchanged in the Recent flora.

CONCLUSIONS

The significance of the fossil pollen data, which I have attempted to show here, thus covers the whole spectrum, from a broad view of the development of the angiosperms as a whole with a first pollen record from the Barremian but probably originating earlier; to the early split between

monocotyledons and dicotyledons; to the split within the dicotyledons between woody Ranales and a more advanced group; to the achievement of dominance in the vegetation by successful competition with gymnosperms and ferns; to the crystallization of most orders of angiosperms in the course of the Cretaceous, and of many modern families and genera in the Cretaceous and Tertiary; and finally to the origin of some modern species in the younger Tertiary.

Of course, any taxon starts as a species, and the connection with the Recent flora just represents a fleeting moment in time, frozen in our Recent taxonomy. To adopt the rules of modern taxonomy to fossil groups takes special care but is possible, as long as we always remember that a taxon is constructed by the independent evolution of character complexes. Wood and pollen evolution, as well as leaf and pollen evolution, thus, have hardly any common factors, but flower and pollen evolution are much more closely linked and it may be argued that much of what we see in the fossil pollen evolution reflects, in essence, the struggle for outbreeding by improvement of the changes for cross pollination.

The palaeobotanical data as a whole show more and more clearly the different timing of first occurrence of characters as well as the shorter or longer period of evolutionary coherence that follows. Clausen and Hiesey (1960) have shown that a genetic basis can be found for the difference between a variable and a uniform period in the life of a taxon, and Gould and Eldredge (1977) have drawn attention to the significance of periods of stasis in their interpretation of the fossil record.

Possibly the pre-magnoliid plants from the early Cretaceous ancestral to Chloranthaceae and Winteraceae have existed for an even longer time than their pollen record indicates.

In general, Chloranthaceae are considered to combine a primitive wood anatomy and pollen morphology with highly reduced and specialized reproductive structures (cf. Stebbins, 1974: 123).

Leroy (1983) has recently challenged the current interpretation of the chloranthaceous flower, which he considers to be primitive and primarily anemophilous. In particular, the strobiloid nature of the male flower of *Hedyosmum* would bring this genus close to the elusive angiosperm ancestors.

In Winteraceae, a more specialized pollen type, which had already evolved in the Aptian/Albian,

is combined with primitive reproductive structures and vesselless wood.

In both cases, it would appear that reproduction has not changed much since the lower Cretaceous and was probably dependant on the same pollinating agents as today.

At the other extreme, we have seen that the 'tubiflorous' families, adapted to specialized insect visitors, and Sonneratia, adapted to bat pollination, are young groups, and that in the latter, 'stasis' in pollen characters has not been achieved yet.

More indirectly, the fossil pollen evidence indicates the younger are of the herbaceous dicotyledons and confirms the predicted correlation with advancement indices.

For the monocotyledons, the secondary development of the woody palms is clearly shown, as well as the young development of Gramineae and Cyperaceae, which may have played a role in the extinction of the Restionaceae in the northern hemisphere.

The recognition of extinct groups of angiosperms on the basis of the pollen record is paralleled by recent palaeobotanical research on macrofossils and tends to challenge further the formerly widely held idea that the middle Cretaceous angiosperm flora contained many modern taxa, some exceptions (*Platanus*) notwithstanding. But even these early extinct groups can be related to present-day taxa and thus incorporated in the body of taxonomic knowledge.

The question of external factors providing periodic impulses for accelerated angiosperm evolution concentrates on the modernization in the Maestrichtian, in which many unrelated taxa appear to be affected. One can think of climatic factors, such as a radiation maximum, decrease of grazing pressure of dinosaurs, and evolution of chemical defenses, to mention a few possibilities. Rather more firmly established is the role of changing climates in the evolution of herbaceous groups in the course of the Tertiary, and the co-evolution with specialized insect and bat groups in the mid-Tertiary.

To a certain extent, the fossil pollen data provide support for a view of angiosperm evolution as a fairly gradual additive process, proposed recently by Tiffney (1981).

Remaining is the mystery of the origin of the angiosperms. If I were bold enough to express an opinion here, I would follow Stebbins (1974) and Doyle (1978) and say that they probably

lived in a semi-arid inland environment in West Gondwanaland, not that they were coastal plants, as recently proposed by Dilcher and Retallack (1981). Thus, the lack of transitional types with gymnosperms, although regrettable, becomes at least understandable.

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